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Understanding how animals respond to and cope with variation in ambient temperature is an important priority. The reason for this is that ambient temperature is a key component of the physical environment that influences offspring performance in a wide range of ectotherms and endotherms. Here, we investigate whether post-hatching parental care provides a behavioral mechanism for buffering against the effects of ambient temperature on offspring in the burying beetle *Nicrophorus vespilloides*. We used a 3×2 factorial design where we manipulated ambient temperature (15, 20 or 25°C) and parental care (presence or absence of a female parent after hatching). We found that the effect of ambient temperature on offspring performance was conditional upon the presence or absence of a caring female. Fewer larvae survived in the absence than in the presence of a caring female at 15°C whilst there was no difference in larval survival at 20 and 25°C. Our results show that parental care buffers against some of the detrimental effects of variation in ambient temperature on offspring. We suggest that post-hatching parental care may buffer against such effects by creating a more benign environment or by boosting offspring resilience towards stressors. Our results have important implications for our understanding of the evolution of parental care because they suggest that the evolution of parental care could allow species to expand their geographical range to colonize areas with harsher climatic conditions than they otherwise would tolerate.

Key words: **ambient temperature, burying beetle, ectotherm, offspring performance, *Nicrophorus vespilloides*, parental care.**

INTRODUCTION

Parental care is defined as any parental trait that increases the fitness of a parent's offspring, often at a cost to the parent's own fitness (Smiseth et al. 2012). Parental care evolved as a mechanism for neutralizing particular environmental hazards to offspring, such as the risks of predation and starvation (Clutton-Brock 1991; Smiseth et al. 2012). For example, it is generally accepted that the risk of predation promoted the evolution of attendance or brooding of eggs and/or juveniles, whilst the risk of starvation promoted the evolution of larger eggs, placentation and parental food provisioning after hatching or birth (Clutton-Brock 1991; Smiseth et al. 2012). There is mounting evidence that, once parental care has evolved, it can buffer against a wide range of hazards to offspring in addition to those that promoted its evolution. For example, in song sparrows (*Melospiza melodia*), post-hatching parental care buffers against the detrimental effects of high precipitation and high population density (Dybala et al. 2013). Meanwhile, in the burying beetle *Nicrophorus vespilloides*, parental care buffers against inbreeding depression in offspring (Pilakouta et al. 2015). Thus, the evolution of parental care may represent a key evolutionary innovation that provides a mechanism whereby parents can buffer against a wide range of environmental hazards that otherwise would be detrimental to their offspring.

Understanding the potential role of parental care as a mechanism for buffering against variation in ambient temperature is an important priority given that extreme weather events, including heat waves, are likely to become more frequent in the near future due to anthropogenic climate change (Stocker et al. 2013). Ambient temperature is a key component of the physical environment that influences various components of

offspring performance, including rate of offspring development, offspring body size and offspring survival in a wide range of ectotherms (Li and Jackson 1996; Lourdais et al. 2004; Wang et al. 2009) and endotherms (Dawson et al. 2005; Paul et al. 2010; de Zwaan et al. 2019). In birds, as well as some reptiles, parents directly buffer against variation in ambient temperature by incubating their eggs (Deeming 2001, 2004). For example, parent birds alter their incubation behavior in response to variation in ambient temperatures (Conway and Martin 2000; Amat and Masero 2004), thereby increasing the growth and survival of their offspring (Hepp et al. 2006; DuRant et al. 2003). However, little is known about parental care as a mechanism for buffering against variation in ambient temperature in ectotherms where parents do not incubate their eggs. As argued above, once parental care has evolved, it may provide parents with a generic mechanism for buffering against environmental hazards to their offspring, including suboptimal ambient temperatures. Here we address this gap by comparing offspring performance at different ambient temperatures in the presence or absence of parental care, using the burying beetle *Nicrophorus vespilloides* as our study system.

The burying beetle *N. vespilloides* breeds on carcasses of small vertebrates, which provide the sole source of food for the developing larvae (Scott 1998). This species is an ideal study system for investigating whether parental care buffers against the effects of ambient temperature on offspring performance. First, given that it is an ectotherm, ambient temperature is likely to have strong effect on the performance of both offspring and parents. Secondly, it has highly elaborate forms of post-hatching care that includes food provisioning to offspring and defense against predators, infanticidal conspecifics and microbial competitors (Eggert et al. 1997; Scott 1998). Third, post-hatching parental care is facultative, which means that it is straightforward to manipulate the presence or

absence of parental care through parental removal experiments (Eggert et al. 1998; Smiseth et al. 2003; Pilakouta et al. 2015). Forth, it is easily bred under laboratory conditions, allowing for careful control of environmental conditions, including ambient temperature, and monitoring of effects on the performance of offspring and their parents (Eggert et al. 1998; Smiseth et al. 2003; Pilakouta et al. 2015).

Here we used a 3×2 factorial design where we manipulated ambient temperature (15, 20 or 25°C) and parental care (presence or absence of a caring female parent after hatching) and monitored subsequent effects on offspring performance (i.e., larval survival and mass). 15°C represents the average summer temperature of our study population, 20°C the standard temperature at which laboratory populations of this species are maintained (Eggert et al. 1998; Smiseth et al. 2003; Pilakouta et al. 2015), whilst 25°C represents the temperature of a potential heat wave in our study area. Prior work shows that offspring perform better in the presence than in the absence of caring parents (Eggert et al. 1998; Smiseth et al. 2003; Pilakouta et al. 2015). Thus, if post-hatching parental care buffers against the effects of variation in ambient temperature, we expected an effect of the interaction between parental care and ambient temperature, reflecting that the presence of a caring parent had a greater effect on offspring performance (survival and/or mass) at 25°C than at 15 or 20°C. We also tested whether parents pay a cost from buffering against the effects of ambient temperature on offspring. If so, we expected an effect of the interaction between parental care and ambient temperature, reflecting a greater difference in parental performance (weight change whilst breeding and post-breeding life span) between caring and non-caring females at 25°C than at 15 or 20°C.

METHODS

Study animals

We used virgin beetles from our outbred laboratory stock population maintained at the University of Edinburgh. This population descended from beetles originally collected in the wild at Corstorphine Hill (55° 56’ 59” N, –3° 16’ 14” E) and Hermitage of Braid (55° 55’ 25” N, –3° 16’ 16” E), Edinburgh, UK. All beetles were kept under 16:8 light:dark conditions and at 20°C. Nonbreeding adults were housed individually in plastic containers (12 × 8 × 2 cm) filled with moist soil and fed organic beef twice a week.

Experimental design and procedures

As mentioned above, we used a 3×2 factorial design where we manipulated both ambient temperature (15, 20 or 25°C) and the presence or absence of a caring female parent after hatching. 15°C matches the baseline summer temperature experienced by our study population (the average temperatures in Edinburgh in June, July and August are 13.5, 15.3 and 15.2°C, respectively; https://en.wikipedia.org/wiki/Edinburgh). 20°C is the baseline temperature under which laboratory populations of this species traditionally are maintained and studied (e.g., Eggert et al. 1998; Smiseth et al. 2003; Pilakouta et al. 2015). The beetles used in our experiments had been kept under laboratory conditions for 9–10 generations. Each generation, we recruited the same number of offspring from each family (3 offspring) to the stock population regardless of the number of offspring each female produced (Mattey et al. 2018). This practice limits adaptation to laboratory

122 conditions, and it is unlikely that our laboratory population were adapted to breeding at
123 20°C. Finally, 25°C represents the conditions of a potential heat wave experienced by our
124 study population (the maximum temperatures in Edinburgh for June, July and August are
125 27.8, 30.0 and 31.4°C, respectively; https://en.wikipedia.org/wiki/Edinburgh). In our
126 study species, adults tend to bury their carcasses shallowly in the leaf litter at the start of
127 breeding (Pukowski 1933). Although, this will buffer against effects of short-term
128 fluctuations in ambient temperatures, breeding beetles will still be susceptible to effects
129 of more persistent variation in ambient temperature. We therefore used a temperature
130 that was somewhat lower than the maximum temperatures to represent a heat wave.

131 We next manipulated post-hatching parental care by either removing both parents
132 on the day of hatching (absence of care) or leaving the female to care for the larvae until
133 they dispersed from the carcass (presence of care). We always removed the male on the
134 day of hatching because male assistance in post-hatching parental care is very variable in
135 *N. vespilloides* and male removal has no effect on larval performance under laboratory
136 conditions (Eggert et al. 1998; Smiseth et al. 2005). Parental removal experiments are
137 used routinely in this species and larvae survive well in the absence of care under
138 laboratory conditions (Eggert et al. 1998; Smiseth et al. 2003; Pilakouta et al. 2015).

139 At the start of the experiment, we randomly paired virgin male and female beetles
140 from our stock population. We placed each pair in a transparent plastic container (17 × 12
141 × 6 cm) filled with 1cm of moist soil. Each pair was provided with a freshly thawed mouse
142 carcass (supplied by Livefoods Direct, Sheffield, UK) with a mean (± 1SE) mass of 22.86g ±
143 1.08 (range: 20–24g). At the time of pairing, we weighed all females, using this
144 information to calculate female weight change whilst breeding (see below). We then

145 placed the containers in an incubator (Qualicool 360L) pre-set to one the three ambient
146 temperatures; that is, 15, 20 or 25°C. We used a temperature probe (Elitech RC-5,
147 London, UK) to monitor ambient temperatures over time (resolution: 0.1°C; accuracy: ±
148 0.5°C). This confirmed that the mean (± SE) of the set temperatures were accurate and
149 fluctuated minimally during the experiment (15°C: mean 14.97°C ± 0.21; 20°C: mean
150 19.96°C ± 0.31; 25°C: mean 24.92°C ± 0.34). For practical reasons, we conducted our
151 experiment across 6 blocks with 2 replicate blocks for each temperature. Within each
152 block, we set up 30 breeding pairs, 15 of which were assigned to each of the two parental
153 care treatments (i.e., presence or absence of care). Thus, the total sample size of our
154 experiment was 180 breeding pairs, with 30 pairs allocated to each of the six treatments.
155 We randomized the order of the temperature treatments.

156 We recorded clutch size as the number of eggs visible through the bottom of the
157 transparent container (Monteith et al. 2012). To this end, we counted the number of eggs
158 twice a day (morning and afternoon) until eggs hatched. In the limited amount of soil we
159 used, the number of eggs visible through the bottom is positively correlated with the
160 actual number of eggs in the clutch (Pearson's correlation: $r = 0.98$, $N = 21$, $P < 0.001$;
161 Monteith et al 2012). We removed both parents on the day of hatching for broods
162 assigned to the 'absence of care' treatment, whilst we only removed the male for broods
163 assigned to the 'presence of care' treatment. We placed the removed females individually
164 in a fresh container (12 × 8 × 2 cm) filled with moist soil. We placed the females back in
165 the incubator to ensure that they were exposed to the same temperature as their
166 offspring and females that cared for their offspring. We provided removed females with
167 organic beef twice a week, as described above for the stock population.

We left all broods to complete their development on the carcass and monitored their subsequent performance. We recorded the date and time of day (morning or afternoon) at which all larvae in a brood dispersed from the carcass. We defined larval dispersal as when all larvae in the brood had left the crypt surrounding the carcass, and normally occurs about 4–6 days after hatching (Smiseth et al. 2003, 2005). We later used this information to calculate larval development time from the date of hatching until the date of dispersal. At dispersal, we counted the number of larvae in the brood and weighed the whole brood. We then calculated mean offspring mass in each brood by dividing brood mass by number of larvae. We transferred the brood to a fresh container filled with moist soil to allow the larvae to pupate and eclose as adults. We always kept these containers at 20°C to ensure that any effect on offspring until eclosion was due to the ambient temperature broods were exposed to during early development on the carcass. At dispersal, we weighed all females again, using this information to calculate weight change whilst breeding as the difference in mass at larval dispersal and the start of breeding. Prior work on this species show that caring females benefit directly in terms of gaining mass by consuming from the resource (e.g., Pilakouta et al. 2016; Paquet and Smiseth 2017; Grey et al. 2018). We then placed females in an individual container to record their life span. At this stage, we always kept females at 20°C to ensure that any effect was due to the ambient temperature females were exposed to whilst breeding. We checked containers with pupae three times a week until pupae eclosed as adult beetles. At the time of eclosion, we counted the number of offspring in each brood that had survived until adulthood. We used this information to calculate offspring survival from dispersal until eclosion.

192 Statistical analyses

193 All statistical analyses were conducted using the package 'car' (Fox and Weisberg 2011) in
194 R v 3.3.3 (R Core Team 2018). We analyzed data on number of eggs laid and larval survival
195 from hatching until dispersal using generalized linear models fitted with a quasi-Poisson
196 error structure to control for overdispersion. We used generalized linear models fitted
197 with a binomial error distribution to analyze data on offspring survival from dispersal to
198 eclosion. We used generalized linear models fitted with Poisson distribution to analyze
199 data on larval development time and female life span given that these response variables
200 were counts of the number of days from hatching until and the number of days until the
201 female died, respectively. Finally, we used general linear models fitted with a Gaussian
202 distribution to analyze data on mean larval mass at dispersal and female weight change.
203 We included clutch size as a predictor in all models to account for potential effects due to
204 variation in the number of eggs laid by different females. For each model, we report
205 likelihood ratios for the overall effect of temperature and the interaction between
206 temperature and parental care using the 'Anova' function in 'car'. We report estimates if
207 effect sizes with SE and z-scores or t-values for the effect of clutch size using the
208 'summary' function. For the remaining factors, we report estimates of effect sizes with SE
209 and z-scores based on Tukey tests using the package 'multcomp'. In the latter case, we
210 used Bonferroni correction to adjust p-values for multiple comparisons (Bretz et al. 2010).
211 All analyses were performed at the level of brood.

212

213 **RESULTS**

As predicted if post-hatching parental care buffered against the effects of ambient temperature, there was a significant effect of the interaction between temperature and parental care on one component of offspring performance: larval survival from hatching until dispersal (Table 1; Figure 1c). However, the pattern of this interaction effect was different to the one we predicted as the presence of a caring parent had a significant effect on offspring performance at 15°C, but not at 20°C or 25°C (Table 1). We next conducted two separate post-hoc tests to investigate in greater detail the buffering effect of post-hatching parental care across our temperature range – one comparing 15 and 20°C and one comparing 20 and 25°C. In both cases, there was a significant effect of the interaction between temperature and parental care (generalized linear models: 15 and 20°C: $LR\chi^2 = 6.304$, $P = 0.012$; 20 and 25°C: $LR\chi^2 = 3.863$, $P = 0.049$). Thus, the presence of a caring female had a greater effect on offspring survival at 15°C than at 20°C and at 25°C than at 20°C (Figure 1c). There were no effects of the interaction between parental care and temperature on larval development time from hatching until dispersal, mean larval mass at dispersal, or larval survival from dispersal to eclosion as an adult (Table 1; Figure 1a, b, d). Finally, there was no evidence that parents paid a cost from buffering against the effects of ambient temperature as there was effect of the interaction between parental care and temperature on either female weight change whilst breeding or female life span after breeding (Table 2; Figure 2).

Ambient temperature had a significant main effect on the performance of both offspring and their female parent (tables 1 and 2). Temperature affected clutch size (generalized linear model: $LR\chi^2 = 16.088$, $P = 0.0003$). Females laid fewer eggs (mean ± SD: 17.27 ± 11.13 eggs) at 25°C than at either 20°C (24.63 ± 10.50 eggs) (Tukey: estimate 0.355 ± 0.101, $z = 3.522$, $P = 0.001$) or 15°C (24.85 ± 12.73 eggs) (Tukey: estimate 0.347 ±

238 0.101, z = 3.436, P = 0.002), whilst there was no difference in number of eggs laid at 15
239 and 20°C (Tukey: estimate –0.008 ± 0.092, z = –0.089, P = 0.999). Ambient temperature
240 affected development time from hatching until dispersal (table 1), with offspring
241 developing faster at 25°C than at 20°C and 15°C, whilst there was no difference in
242 development time between 15°C and 20°C (Table 1; Figure 1a). Ambient temperature also
243 affected mean larval mass at dispersal (Table 1). Mean larval mass was higher at 20°C
244 than at either 15 or 25°C, whilst there was no difference in mean larval mass at 15 and
245 25°C (Table 1; Figure 1b). Furthermore, ambient temperature affected number of larvae
246 that survived from hatching until dispersal (Table 1). There were fewer larvae at 25°C
247 than at either 15 or 20°C, whilst there was no difference in number of larvae at 15 and
248 20°C (Table 1; Figure 1c). Ambient temperature affected female weight change from the
249 onset of breeding until larval dispersal (Table 2). Females gained more weight whilst
250 breeding at 15°C than at either 20 or 25°C, but there was no difference in female weight
251 change whilst breeding at 20 and 25°C (Table 1; Figure 2a). Ambient temperature had no
252 effects on offspring survival from dispersal until eclosion as an adult (Table 1; Figure 1d)
253 or female life span after breeding (Table 2; Figure 2b).

254 Post-hatching parental care had a positive main effect on mean larval mass,
255 number of larvae at dispersal, and offspring survival from dispersal until eclosion (Table 1;
256 Figure 1b–d). There was also a difference in weight change whilst breeding between
257 caring and non-caring females (Table 2). Caring females tended to gain weight whilst
258 breeding whilst non-caring females tended to lose weight (Figure 2a). Post-hatching
259 parental care had no effect on offspring development time (Table 1; Figure 1a) and there
260 was no difference in life span after breeding between caring females and females that
261 had been removed (Table 2; Figure 2b).

DISCUSSION

We found that the presence of a caring female had a significant effect on offspring performance at 15°C but not at 20 or 25°C. This finding has important implications by showing that the benefits of post-hatching parental care to offspring are temperature dependent. One potential explanation for why the benefits of parental care may be temperature dependent in ectotherms is that their performance tend to increase with rising temperatures until reaching an optimum after which performance declines rapidly until reaching the critical thermal maximum (Huey and Stevenson 1979; Stillman 2003; Deutsch et al. 2008). Unfortunately, there are no thermal performance curves for our study species. Nevertheless, based on the explanation suggested above, we anticipated offspring performance to peak at 25°C given that this temperature is near or below the critical thermal maximum for most insects (24–40°C; Deutsch et al. 2008; Martin and Huey 2008; Estay et al. 2013). Thus, our finding that offspring performance peaked at 15 or 20°C provides no support for this explanation. An alternative explanation for our finding is that, whilst breeding on carcasses of small vertebrates, larvae compete with microbes for access to resources (Rozen et al. 2008). Given that ambient temperature also determines decay of carrion due to microbial growth (Xu et al. 2016), the finding that larval survival was lowest at 25°C suggests that ambient temperature may have had a differential effect on the competitive ability of larvae and microbes. Furthermore, given that caring parents are known to suppress microbial growth in this species (Rozen et al. 2008), the effect of the interaction between ambient temperature and parental care suggests that the presence of a caring female had a differential effect on the outcome of

competition between larvae and microbes depending on the ambient temperature. Further work is now needed to investigate this suggestion.

We found that larval survival from hatching until dispersal was highest at 15°C in the presence of a caring parent. Given that 15°C closely matches the average daily summer temperatures in the study area and parents normally provide care for their broods, this suggests that larvae of our population are well adapted to the conditions normally encountered in the wild. We also found that the larvae had substantially lower survival in the absence than in presence of a caring female at 15°C. This finding has important implications by suggesting that the evolution of elaborate post-hatching parental care has allowed this species to extend its geographical range to areas with a colder climate than it otherwise would tolerate. A recent study on another species within the genus *Nicrophorus*, *N. sayi*, suggests the evolution of post-hatching parental care has allowed this species to shift its seasonal activity by breeding under cold conditions in early spring, potentially as a means to avoid competition for resources with its congeners (Benowitz et al. 2019). Thus, although post-hatching parental care in this genus is thought to have evolved in response to inter- and intraspecific competition over carrion (Eggert and Müller 1997; Scott 1998), the generic buffering capacity of parental care may have allowed these species to expand their geographical range and/or seasonal activity. This suggestion has important implications for our understanding of the evolution of post-hatching parental care by providing a potential explanation for why it tends to be obligate in most species. The reason for this is that any expansion of geographical range or seasonal activity to environmental conditions that otherwise cannot be tolerated would effectively prevent any secondary losses of post-hatching parental care.

Our study raises questions about the potential mechanisms for how caring parents may buffer against the effects of variation in ambient temperature on offspring performance. In birds and some reptiles, parents can directly buffer against variation in ambient temperature by incubating their eggs (Deeming 2001, 2004), but this mechanism is not available for our study species given that parents do not incubate their eggs. We propose three mechanisms for how parental care might provide a generic mechanism for buffering against suboptimal ambient temperatures: (1) parents facultatively adjust the amount of care they provide in response to variation in ambient temperature, thereby compensating for any detrimental effects at suboptimal temperatures, (2) caring parents create a more benign environment that minimizes effects of other hazards to the offspring, such as the risks of starvation or infection, thereby buffering against any detrimental effects at suboptimal temperatures, and (3) parents enhance their offspring's growth and condition, thereby facilitating the offspring's own ability to cope with the otherwise detrimental effects at suboptimal temperatures. If females provided more care at 15°C as compared to 20 and 25°C, we expected the former females to pay some cost in terms of loosing more mass (or gaining less) or a shorter life span. In contrast, we found no effect of the interaction between ambient temperature and parental care influenced female performance (i.e., female weight change whilst breeding or life span after breeding). Thus, we found no evidence in support for the first explanation, suggesting that the buffering effect of post-hatching parental care is independent of any plastic responses by parents to changing temperature. Our results cannot differentiate between the second and third explanation. Nevertheless, we found that post-hatching parental care had a positive impact on mean larval mass, lending some tentative support for the

third mechanism. There is now need for further work to investigate the mechanistic basis for how caring parents buffer against the effects of thermal stress on their offspring.

Finally, our results have implications for our understanding of the potential role of parental care as a behavioral mechanism for mitigating the detrimental effects of rising temperatures due to anthropogenic climate change. Prior work has focused on how individuals alter their own behavior in response to rising temperatures, thereby mitigating some of the detrimental effects of climate change to themselves (Kearney et al. 2009; Beever et al. 2017). Here we show that post-hatching parental care – a social behavior that is expressed in parents but that affects the offspring's fitness – can mitigate some of the effects of ambient temperature on offspring performance. There is now a need for further studies that extend our work to other taxa with parental care or similar social behaviors that might buffer against climate change and that expand our manipulations to a wider range of temperatures. Furthermore, there is a need for comparative work examining whether social species are better at coping with thermal stress associated with climate change than solitary ones.

In conclusion, we show that post-hatching parental care buffered against the effects of ambient temperature on offspring performance, and that this buffering effect may be independent of any plastic responses by parents to changing temperature. Instead, post-hatching parental care may buffer against the effects of ambient temperature by creating a more benign environment for the offspring or by boosting the offspring's condition and thereby their resilience towards stressors. Our results highlight the need to understand how parental care and other social behaviors may determine how

353 well animal populations respond to and cope with extreme weather conditions, the
354 frequency of which is expected to increase due to anthropogenic climate change.

355

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362 Data accessibility: Analyses reported in this article can be reproduced using the data
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364

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466 **Table 1**

467 **General linear and generalized linear models testing for effects of ambient temperature (15, 20 or 25°C), post-hatching parental care**
468 **(presence or absence of caring parents) and the interaction between them on four measures of offspring performance: development time**
469 **from hatching to dispersal, mean mass at dispersal, number of offspring at dispersal, and survival from dispersal to eclosion. All test**
470 **statistics are z-scores, expect for the overall effect of temperature and the interaction between temperature and parental care, which are**
471 **likelihood ratios ($LR\chi^2$) (indicated by *) and for the effect of clutch size on mean mass at dispersal and number of offspring at dispersal,**
472 **which are t-values (indicated by †). See main text for further details on the statistical analyses.**

Development time from hatching to dispersal	Estimate	SE	Test statistic	*P*-value
Temperature			20.574*	<0.0001
15°C vs. 20°C	0.061	0.087	0.695	0.764
15°C vs. 25°C	0.371	0.116	3.203	0.004
20°C vs. 25°C	0.310	0.116	2.639	0.022
Parental care (present vs. absent)	–0.048	0.083	–0.577	0.564
Clutch size	0.0005	0.003	0.193	0.847
Temperature*Parental care			0.346*	0.841
15°C present vs. 15°C absent	–0.031	0.081	–0.381	0.999

20°C present vs. 20°C absent	–0.048	0.083	–0.577	0.992
25°C present vs. 25°C absent	0.041	0.128	0.321	>0.999
Mean mass at dispersal				
Temperature			15.808*	0.0004
15 vs. 20°C	–0.027	0.020	–2.657	0.021
15 vs. 25°C	0.012	0.012	1.036	0.552
20 vs. 25°C	0.039	0.012	3.252	0.003
Parental care (present vs. absent)	0.054	0.009	4.860	<0.0001
Clutch size	0.042	0,006	7.563†	<0.0001
Temperature*Parental care			2.911*	0.233
15°C present vs. 15°C absent	0.068	0.009	7.215	<0.0001
20°C present vs. 20°C absent	0.046	0.009	4.860	<0.0001
25°C present vs. 25°C absent	0.060	0.013	4.799	<0.0001
Number of offspring at dispersal				
Temperature			37.481*	<0.0001
15°C vs. 20°C	–0.417	0.206	–2.020	0.102
15°C vs. 25°C	1.193	0.374	3.192	0.0038
20°C vs. 25°C	1.610	0.360	4.475	<0.001

Parental care (present vs. absent)	–0.058	0.181	–0.318	0.751
Clutch size	0.042	0.006	7.563†	<0.0001
Temperature*Parental care			7.622*	0.022
15°C present vs. 15°C absent	0.578	0.196	2.946	0.034
20°C present vs. 20°C absent	–0.058	0.181	–0.318	>0.999
25°C present vs. 25°C absent	0.801	0.399	2.007	0.320
Survival from dispersal to eclosion				
Temperature			5.289*	0.071
15°C vs. 20°C	0.996	0.702	1.420	0.327
15°C vs. 25°C	–0.496	0.925	–0.537	0.852
20°C vs. 25°C	–1.492	0.919	–1.625	0.232
Parental care (present vs. absent)	1.792	0.724	2.474	0.013
Clutch size	0.022	0.028	0.811	0.418
Temperature*Parental care			0.602*	0.740
15°C present vs. 15°C absent	2.389	1.222	1.955	0.353
20°C present vs. 20°C absent	1.792	0.724	2.474	0.123
25°C present vs. 25°C absent	–0.299	0.939	0.319	0.958

473

474 **Table 2**

475 **General linear and generalized linear models testing for effects of ambient temperature (15, 20 or 25°C), post-hatching parental care**
476 **(presence or absence of caring parents) and the interaction between them on two measures of the performance of the female parent:**
477 **weight change from start of breeding until larval dispersal, and life span. All test statistics are z-scores, expect for the overall effect of**
478 **temperature and the interaction between temperature and parental care, which are likelihood ratios ($LR\chi^2$) (indicated by *) and for the**
479 **effect of clutch size on weight change, which is a t-value (indicated by †). See main text for further details on the statistical analyses.**

Weight change	Estimate	SE	Test statistic	*P*-value
Temperature			28.223*	<0.0001
15°C vs. 20°C	0.028	0.009	2.904	0.010
15°C vs. 25°C	0.052	0.011	4.939	<0.001
20°C vs. 25°C	0.024	0.011	2.203	0.070
Parental care (present vs. absent)	0.034	0.010	3.599	0.0003
Clutch size	–0.0005	0.0003	–1.757†	0.081
Temperature*Parental care			3.540*	0.170
15°C present vs. 15°C absent	0.021	0.009	2.273	0.204
20°C present vs. 20°C absent	0.034	0.010	3.599	0.004

25°C present vs. 25°C absent	0.048	0.011	4.427	<0.0001
Life span				
Temperature			3.782*	0.151
15°C vs. 20°C	–0.003	0.033	–0.076	0.997
15°C vs. 25°C	0.063	0.037	1.732	0.193
20°C vs. 25°C	0.066	0.038	1.747	0.187
Parental care (absent vs. present)	–0.020	0.032	–0.613	0.540
Clutch size	0.002	0.0009	2.294	0.022
Temperature*Parental care			3.502*	0.174
15°C present vs. 15°C absent	0.041	0.032	1.284	0793
20°C present vs. 20°C absent	–0.020	0.033	–0.613	0.990
25°C present vs. 25°C absent	0.069	0.038	1.834	0.442

480

481 **Figure legends**

482

483 **Figure 1**

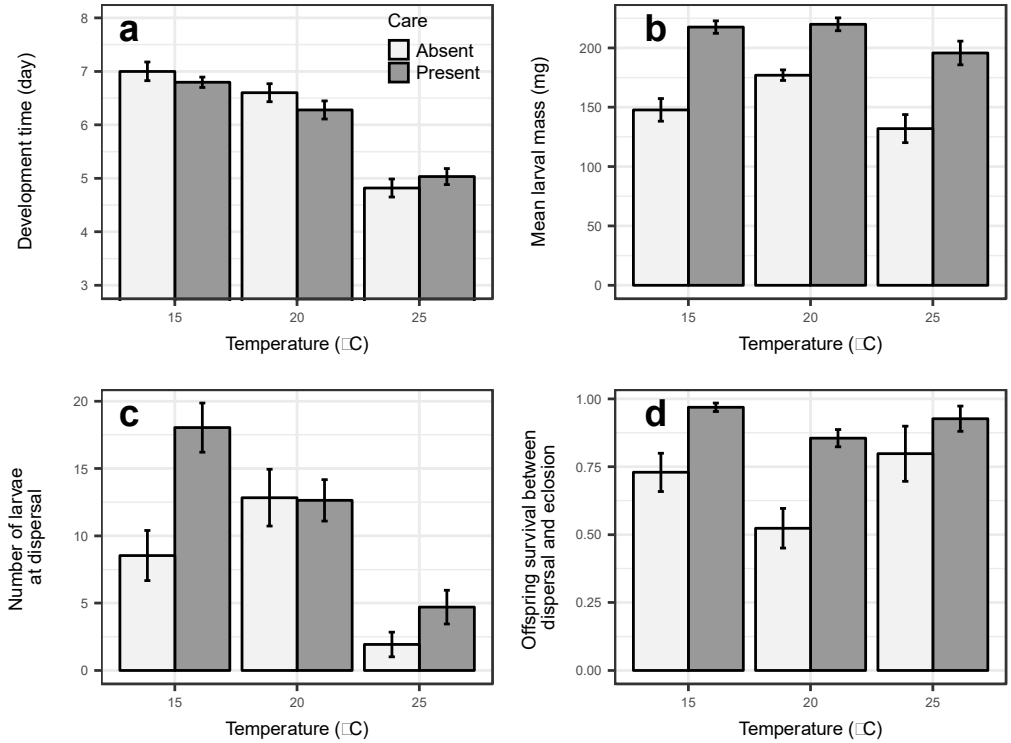
484 Effects of ambient temperature (15, 20 or 25°C), post-hatching parental care (presence or
485 absence of caring parents) and the interaction between them on four measures of
486 offspring performance: development time from hatching to dispersal (a), mean mass at
487 dispersal (b), number of offspring at dispersal (c), and survival from dispersal to eclosion
488 (d). Drawn from raw data and representing means ± 1 SE. The sample sizes for
489 development time from hatching to dispersal, mean mass at dispersal and survival from
490 dispersal to eclosion were: 15°C and female present (*N* = 27), 15°C and female absent (*N* =
491 19), 20°C and female present (*N* = 27), 20°C and female absent (*N* = 20), 25°C and female
492 present (*N* = 15), and 25°C and female absent (*N* = 11). The sample sizes for number of
493 offspring at dispersal were: 15°C and female present (*N* = 29), 15°C and female absent (*N*
494 = 28), 20°C and female present (*N* = 30), 20°C and female absent (*N* = 30), 25°C and
495 female present (*N* = 28), and 25°C and female absent (*N* = 29).

496

Figure 2

Effects of ambient temperature (15, 20 or 25°C), post-hatching parental care (presence or absence of caring parents) and the interaction between them on female weight change whilst breeding (a) and female life span after breeding (b). Drawn from raw data and representing means ± 1 SE. The sample sizes for weight change were: 15°C and female present (*N* = 27), 15°C and female absent (*N* = 26), 20°C and female present (*N* = 28), 20°C and female absent (*N* = 23), 25°C and female present (*N* = 22), and 25°C and female absent (*N* = 17). The sample sizes for life span were: 15°C and female present (*N* = 26), 15°C and female absent (*N* = 25), 20°C and female present (*N* = 27), 20°C and female absent (*N* = 22), 25°C and female present (*N* = 21), and 25°C and female absent (*N* = 17).

509 Figure 1



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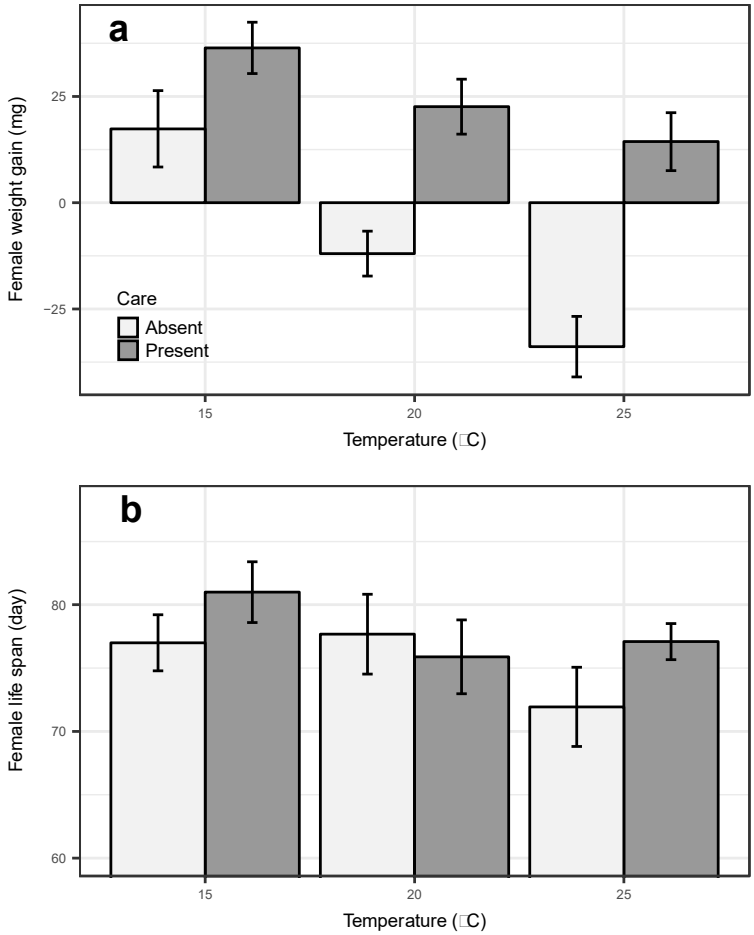
511

512 Figure 2



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